A SYNOPSIS OF THE BURROWING LAND CRABS OF THE WORLD AND LIST OF THEIR ARTHROPOD SYMBIONTS AND BURROW ASSOCIATES

By Donald B. Bright[1] and Charles L. Hogue[2]

Abstract: The burrowing land crabs of the world are defined as an ecological group and the burrow or crabhole faunal community is recognized and discussed as such.

Introductory remarks on terminology, relationship of the crabhole habitat to other habitat types, general physical nature of the crabhole, and the major ecological structure of the community as now known are presented. The remainder of the paper consists of two parts: 1) A list of all the species of borrowing land crabs of the world, including notations on distribution, recognition, and ecology. Twenty-four species in the genera *Sesarma, Ocypode, Uca, Ucides, Gecarcoidea, Cardisoma,* and *Gecarcinus* are given. 2) A list of all published records of arthropods found in crab burrows either associated with the crab as a burrow coinhabitant or having symbiotic relationships with it. The vast majority of these are insects, primarily mosquitoes, of which 140 species are noted. For each burrow associate or symbiont, the distribution, recorded crab host, type of relationship (specific, semispecific, transient or accidental) are given.

INTRODUCTION

The present paper represents a literature survey to establish the present state of knowledge on the unique ecological relationship existing between burrowing land crabs and a variety of associated organisms. From our own field studies it is evident that there are many unrecorded species of arthropods occurring in crabholes and undescribed ecological phenomena to be discovered and analyzed. We hope that from this beginning other workers will recognize the land crab burrow as a special habitat and respond to the need for inquiring further into its natural history.

Published data on land crabs consists primarily of species accounts and selected aspects of behavior and natural history; no broad coverage of the basic ecology of any species exists. Likewise, with regard to the burrow associates, no general ecological treatment is available, only taxonomic notes and fragmentary collecting data.

We are presently engaged in a project to study the biology of land crabs and their burrow associates (Hogue and Bright, 1969). One preliminary field survey in Kenya, East Africa (Hogue and Bright, 1971) has been reported. Field studies in Costa Rica, Baja California, Pacific mainland

[1]Donald B. Bright, Associate Professor of Biology, California State Colege, Fullerton, California 92631.

[2]Charles L. Hogue, Senior Curator of Entomology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

Mexico, Panama, Peru, Ecuador, Western Caribbean (Islas San Andrés and Providencia), and Australia will be reported upon in forthcoming papers. All specimens and data collected on this project are given the code LCBA (Land Crab Burrow Associates). Entomological materials are deposited in the Los Angeles County Museum of Natural History, and crustaceans in the Department of Biology, California State College, Fullerton.

DEFINITIONS

Since we make use of terms and concepts originally devised for very different community types, we find it necessary to define certain of our present usages:

Crabhole and crab burrow: Used synonymously.

Burrowing land crab: This term refers to a group of tropical species which dig well-defined burrows above the normal flooding and flushing action of the tides. These species belong to the families Gecarcinidae, Ocypodidae, and Grapsidae. The family Coenobitidae is excluded since the terrestrial hermit crabs are non-burrowers. Thus our attention will be directed to the following taxa:

Gecarcinidae (all 3 genera of the family)
- *Gecarcoidea*, all species
- *Cardisoma*, all species
- *Gecarcinus*, all species

Grapsidae (only 1 of 26 genera in the family)
- *Sesarma*, certain species only

Ocypodidae (3 of 4 genera in the family)
- *Ocypode*, certain species only
- *Uca*, certain species only
- *Ucides*, certain species only

Several species of land dwelling lobsters (e.g., *Thalassina*), crayfish (*Procambarus, Cambarus*) and freshwater crabs (*Sudanonautes*) also construct burrows supporting an associated fauna. Though we consider these outside our specified limits with burrowing land crabs (and they are omitted from the section on burrowing land crabs), we mention them in our survey of associates because they occur sympatrically with burrowing land crabs and confusion frequently arises in identifying the true owner of a burrow (Scharff and Tweedie, 1942).

Ecological structure of crabhole community: All of the organisms found in the crabhole and associated ecologically with land crabs we refer to as the crabhole community. It is presently possible to evaluate only the gross community structure of arthropod symbionts and burrow associates of land crabs in terms of the general levels of interrelationships and the most conspicuous variations in niches displayed by the arthropod fraction. By niche we mean the total ecological role a species plays in the community, both in regard to its habitual location of occurrence (place niche—microhabitat)

and its inter-dependency with other members of the community (functional niche).

Within the crabhole community we find two general levels of interspecific reaction: The first of these, simple *association*, is shown by the assemblage of species whose common occurrence is dictated directly by the spectrum of indigenous limiting factors (physical and biotic) encountered in the crabhole. The second, *symbiosis*, refers to those species not only tied together by these factors but which also depend directly upon some form of intimate (often or usually also involving prolonged physical contact) interaction with one other member of the community, i.e., parasitism or commensalism (no example of mutualism yet having been found). A summary of the general ecological structure of the arthropod fraction of the crabhole community is given in Table 1.

The extent to which a particular organism is dependent on the crabhole as a suitable habitat and to which it is an obligate member of the crabhole community may be further classed:

I. *Specific* (or obligatory)

The species is narrowly adapted to conditions in the crabhole or lives symbiotically with the host or other community member. Such species have specific adaptations to the physical and biological stresses encountered in the burrow (the precise nature of and adaptive significance of which are

TABLE 1

SUMMARY OF THE KNOWN ECOLOGICAL STRUCTURE OF THE CRABHOLE COMMUNITY (ARTHROPOD FRACTION)

Level of Interspecies Reaction	Niche		Major Examples
	Place	Functional	
ASSOCIATION	Burrow water	Developing; feeding, breeding, etc.	Immature mosquitoes
			Diving beetles (*Bidessus*)
			Cyclops
	Burrow chambers and surface of burrow water	Resting, mating, etc.	Adult mosquitoes
			Adult biting gnats (*Culicoides*)
SYMBIOSIS			
Parasitism	Gill chamber of *Gecarcinus lateralis*	Attaching and feeding	Mite (*Laelaps cancer*)
Commensalism	Peribuccal cavity and renal grooves of *Gecarcinus ruricola*	Attaching to host and feeding on food debris	*Drosophila carcinophila*

presently little known, such as prolonged developmental period, impermeable cuticle, reduced salt absorbing organs, etc.). Examples occur among the following genera: *Deinocerites, Aedes* (*Cancraedes and Geoskusea*), and *Drosophila.*

II. *Semispecific* (or semiobligatory)

The species usually inhabits the crabhole, being adapted at least in part to certain of its conditions but survives well in other habitats. An example is the mosquito *Aedes* (*Skusea*) *pembaensis* which habitually breeds in crabholes but also develops commonly in various other types of coastal ground water accumulations (pools, swamps and even in artificial containers).

III. *Transient* (or facultative)

The species usually inhabits other sites but may take up temporary residence or breed in the crabhole because of its similarity or proximity to the normal habitat. Examples are the many mosquitoes occurring along the seashore such as *Aedes* (*Neomacleaya*) *panayensis* and *Aedes* (*Ochlerotatus*) *taeniorhynchus*; insular treehole breeders, *Aedes* (*Stegomyia*) *polynesiensis*; and indiscriminate breeders, *Culex (Culex) annulirostris.*

IV. *Accidental*

The species is adapted to another habitat and only rarely occurs in and about crabholes for some anomalous reason (e.g., larvae flushed from ground pools during heavy rains, wind blown adults, etc.). For example, adults of *Mansonia* mosquitoes are sometimes found in crabholes but do not develop from larvae and pupae living in the burrow; these mosquitoes require certain aquatic plants to which they attach with special respiratory structures for extracting vascular oxygen. These plants live only in open freshwater pools and ponds.

These four categories of habitat dependence, of course, are provisional. Unfortunately, for no species do we yet know the complete story of its functional niche in the crabhole community.

GENERAL PHYSICAL NATURE OF THE HABITAT

While there is considerable specific variation, in general the land crab burrow is a gently sloping or near vertical tubular excavation ranging from depths of 1.5-3.4 m. The diameter generally is equivalent to the carapace width of the host crab and the depth is determined by the level of the water table.

Normally, the bottom of the burrow is filled with water derived indirectly from ground seepage from nearby sources (streams, estuaries, ponds, open sea, etc.) or directly from rainfall. Thus the water may vary considerably in solute concentrations even from day to day or hour to hour. Like estuarine organisms in general, which are able to accommodate to such changes physiologically, crabhole water dwellers have wide osmoregulatory capacities. Some species, in genera such as *Gecarcinus*, are so well adapted to terres-

triality that their burrows often are for physical protection only and penetration to the water table to maintain a supply of water for physiological functions is not necessary. The community of these shallow burrows, lacking the aquatic fraction, is depauperate.

The burrows are located most often in compact alluvial soil well above high tide lines but still close enough to the sea to permit migration for spawning and close enough to a ground water source to maintain a reservoir. Burrows also are often found along large rivers far inland where the fresh water affords the crab's hydrobiotic needs.

LAND CRABS OF THE WORLD

The following genera and species accounts are for those burrowing land crabs listed as hosts in the arthropod portion of this paper or those, based on our field experience, that are likely to be additional hosts.

In several of the species accounts there is question regarding reliable taxonomic and zoogeographic data. This is particularly true for distributional patterns in the Indo-Pacific, e.g., the species of *Cardisoma* and *Sesarma*. (See Tweedie (1950) for a discussion of the problems associated with *Cardisoma*.) Correspondence with a number of workers indicates that revisions are in preparation for *Sesarma, Uca* and *Gecarcinus*. These works should aid future studies on the distribution of land crabs and their burrow associates.

No attempt has been made to provide a complete synonymy. Where there is considerable taxonomic confusion a note to clarify our usage has been included in the species accounts.

In listing the various species we have assumed that the published reports on burrow ownership are correct. Where authors were unable to identify the crustacean but provide descriptions, specific localities and/or habitats, we have sometimes made a provisional determination. It is hoped that in future accounts authors will attempt to determine hosts specifically and include additional remarks on general ecology of the crab and its associates.

The species we define as land crabs are enumerated below followed by a synopsis of important information on each species.

Family: Grapsidae

1. *Sesarma* (*Sesarma*) *sulcatum*
2. *Sesarma* (*Sesarma*) *meinerti*
3. *Sesarma* (*Chiromantes*) *africanum*
4. *Sesarma* (*Holometopus*) *ortmanni*
5. *Sesarma* (*Holometopus*) *eulimene*

Family: Ocypodidae

6. *Ocypode gaudichaudii*
7. *Ocypode occidentalis*
8. *Ocypode quadrata*
9. *Ocypode ceratophthalma*

10. *Uca pugilator*
11. *Uca subcylindrica*
12. *Uca tangeri*
13. *Ucides cordatus*
14. *Ucides occidentalis*

Family: Gecarcinidae

15. *Gecarcoidea humei*
16. *Cardisoma guanhumi*
17. *Cardisoma crassum*
18. *Cardisoma armatum*
19. *Cardisoma carnifex*
20. *Cardisoma hirtipes*
21. *Gecarcinus planatus*
22. *Gecarcinus ruricola*
23. *Gecarcinus quadratus*
24. *Gecarcinus lateralis*

Family GRAPSIDAE

Genus *Sesarma* Say, 1817

CHARACTERS: Carapace squarish; sides generally straight and parallel; orbits of eye deep, oval and occupy only slightly less than half of the anterior border of the carapace; antennules transverse; epistome well defined; chelipeds thick, and subequal in male, and third pair of legs longest.

DISTRIBUTION: Tropical and subtropical coastal areas of the world.

HABITAT: Coastal marshes, mud flats, banks of drying streams, gravelly mud along lagoons and mangroves.

HABITS: Generally these have well defined burrows which are similar to those of most *Cardisoma* juveniles. These burrows are in muddy, mud-gravel areas extending from the surface down 1 m to the water table. Some do not construct burrows but live under debris (rocks and roots). Most individuals are solitary. In some areas young live in the same burrow with an adult.

REFERENCES[1]: Bott, 1955 (D,T); Campbell, 1967 (D,T); Crane, 1947 (B,D,T,); Crosnier, 1965 (D,T); Gordon, 1934 (D); Macnae, 1966 (B,D); Miers, 1880 (D); Rathbun, 1914 (T); Tesch, 1917 (D,T); Tweedie, 1940 (D,T).

Note: Considerable taxonomic confusion prevails in this taxon, particularly the validity of the subgeneric groupings. Many synonymies are suspected

[1]The application of each reference is indicated by a symbol following (T—taxonomy; B—biology, i.e., habits, habitat, life history, physiology; D—distribution; G—general).

because of the inordinate number of species, e.g., 115 in the Indo-Pacific alone. Campbell (1967) and Crosnier (1965) give recent accounts dealing with these problems. Because of the above, some species determinations are questionable.

1. *Sesarma* (*Sesarma*) *sulcatum* Smith, 1870

COLOR: Carapace and legs dark brownish gray; lower portion of male chelae cream yellow; chelae in females cream with a few maroon striations; females with conspicuous yellow line across front.

DISTRIBUTION: Pacific coast of the Americas (San Ignacio Lagoon, Baja California to southern Panama).

HABITAT: Gravelly mud along lagoon shores, tidal marshes, and on the banks of streams and mangroves.

HABITS: They construct straight or slightly sloped burrows or live under debris characteristic of the habitat. Some spend considerable time climbing the branches of marsh plants, e.g., *Sueda, Salicornia* (Baja California) and the roots and pneumatophores of mangroves, e.g., *Rhizophora* and *Avicennia* (Costa Rica and Panama). Individuals are solitary, but in areas where burrow structure is not well developed they tend to occur in groups, e.g., three to six individuals under a rock (Wright, 1966). In drier habitats they commonly use burrows (occupied and unoccupied) of other crabs, e.g., *Cardisoma crassum*, *Ucides occidentalis* and *Uca* spp. They are often sympatric also with *Goniopsis pulchra*. They are active throughout most of the day (except in drier areas) feeding primarily on plant materials.

COMMON NAMES: Mangrove crab; Marsh crab; Speckled crab.

REFERENCES: Bott, 1955 (D,T); Crane, 1947 (B,D,T,); Garth, 1960 (D); Wright, 1966 (G).

2. *Sesarma* (*Sesarma*) *meinerti* de Man, 1887

COLOR: Carapace black to gray or purple to deep violet, anterior and lateral margin bordered with orange to light yellow; underside a dirty yellow; and chelipeds a striking brilliant red. Cott (1930) gives a good account of this plus a consideration of the theory of warning colors.

DISTRIBUTION: Andamans and Madras, Mozambique, Mauritius, Madagascar; east coast of Africa (south to Port St. John's); across Indo-Pacific to Australia (Cooktown) and north to the Philippines.

HABITAT: Sandy-clay areas and higher, drier, muddy banks associated with estuaries and mangroves.

HABITS: Burrows are well developed and most common in areas where there is dry, relatively hard mud. The burrows are deep and usually extend to the water table. Often the mouth of the burrow has a hood built of mud excavated while enlarging the tunnel or cleaning out. These crabs are retiring, remaining at the mouth of the burrow, and only leave to forage at night. They apparently feed primarily on plant material, but also act as scavengers where

they occur in high density. There is no indication of colonialism in areas of high density.

COMMON NAME: Marsh crab?

REFERENCES: Alcock, 1900 (D,T); Chace, 1953 (D,T); Cott, 1930 (G); Crosnier, 1965 (D,T); Hogue & Bright, 1971 (D); Macnae, 1966 (B,D); Millard and Harrison, 1954 (G).

3. *Sesarma* (*Chiromantes*) *africanum* H. Milne Edwards, 1837

COLOR: Carapace reddish brown; transverse patches of stiff hairs over carapace and limbs; distal portion of chelae violet-red in color.

DISTRIBUTION: Senegal to Benguela, Angola; also Barbados(?).

HABITAT: Mangroves; salt marshes; and mouths of rivers.

HABITS: Occurs primarily in dense, well shaded areas of mangroves. Juveniles and adults are conspicuous, climbing over vegetation, since they have no burrows or only very small ones. Typically, when threatened, they hide under debris and roots. In open localities, with soft mud, they construct shallow (.3-.6 m) individual burrows. These burrows are not known to intersect. They are presumed to be scavengers.

COMMON NAME: Hairy lagoon crab.

REFERENCE: Rathbun, 1921 (D,T).

4. *Sesarma* (*Holometopus*) *ortmanni* Crosnier, 1965

COLOR: Carapace greenish brown and heavily calcified; chelae a dull to bright orange.

DISTRIBUTION: East coast of Africa; Madagascar.

HABITAT: Muddy soil along the margins of mangroves.

HABITS: Constructs shallow burrows among exposed pneumatophores of the mangrove, *Avicennia*.

COMMON NAME: None recorded.

REFERENCES: Crosnier, 1965 (D,T); Macnae and Kalk, 1969 (B,D).

5. *Sesarma* (*Holometopus*) *eulimene* de Man, 1898

COLOR: Carapace dull brown and with conspicuous pits; underside a dirty white, chelae of male bright orange-red.

DISTRIBUTION: East coast of Africa from Malindi to Durban.

HABITAT: Mud areas of salt marshes and mangroves.

HABITS: Poorly known. Burrows generally well developed, but shallow, and often associated with the pneumatophores of mangroves. Millard and Harrison (1954) indicate extensive distribution of this species in Richards Bay, South Africa, in areas along the mangrove margins where there is deep, soft mud covered at least once per day by tidal flux.

COMMON NAME: None recorded.

REFERENCES: Barnard, 1947 (D,T), 1950 (D,T); Crosnier, 1965 (D,T); Macnae and Kalk, 1969 (B,D); Millard and Harrison, 1954 (G).

Family OCYPODIDAE

Genus *Ocypode* Fabricius, 1798

CHARACTERS: Carapace deep, somewhat broader than long but generally squarish; orbits large and divided into two chambers; eye stalk often prolonged as a style; antennae small and rudimentary; epistome small; chelipeds shorter than legs and subequal; 4th pair of legs shorter and thinner than others.

DISTRIBUTION: Tropical and subtropical coast of American Atlantic (Rhode Island to Brazil), Mediterranean Sea, coasts of Africa, Red Sea, Indo-Pacific, and eastern Pacific (Turtle Bay, Baja California to Chile).

HABITAT: Sandy beaches with tidal surge; rubble flats; sand-mud areas adjacent to mangrove swamps.

HABITS: Construct simple to complex burrows in the soft substratum of the habitat. In several areas species occur sympatrically but generally are distinguishable on the basis of feeding habits or the presence-absence-degree of development of the style over the eye.

REFERENCES: Alcock, 1900 (D,T); Chace and Hobbs, 1969 (G); Crane, 1941b (B); Garth, 1960 (D); Rathbun, 1918 (D,T); Tweedie, 1950 (D,T).

6. *Ocypode gaudichaudii* H. Milne Edwards & Lucas, 1843

COLOR: Highly variable, coral red to dark brown. Individual color associated with size, sex and the color of substratum of the habitat.

DISTRIBUTION: Pacific coasts of America. Gulf of Fonseca, El Salvador, to Chile; Galapagos Islands.

HABITAT: Common on sandy beaches of protected bays; occasionally on exposed sandy areas when the surge is not high; also occurs along the shores of lagoons.

HABITS: Burrows highly variable; Crane (1941) indicates three types: 1) shallow, simple, oblique; 2) straight with a right angle at 1-3 m depth; and 3) straight for 15-20 cm then extending downward in a gradual spiral. The second type is most common in the center of the range of distribution. All are diurnal and most active following high tide and before flooding midtide. Occasionally occurs sympatrically with *O. occidentalis*. These two species are distinguishable by: 1) *O. gaudichaudii*: carapace length of 17 mm or more and with well developed ocular styles; actively manipulate the substratum feeding on microscopic organic matter (similar to several species of *Uca*); 2) *O. occidentalis*: no ocular style; they are confirmed predators and/or scavengers.

COMMON NAMES: Cart-driver; Carretero (Peru).

REFERENCES: Bott, 1955 (D,T); Crane, 1941b (B); Garth, 1948 (D,T); Rathbun, 1918 (D,T).

7. *Ocypode occidentalis* Stimpson, 1862

COLOR: Upper surface of body and legs generally darkish gray with white marbling. Manus of chelipeds, tips of walking legs and underside of body

cream white. Colors tend to vary with substratum except where sand is volcanic (dark black). These crabs are, due to color, conspicuous when found on light colored or dry sand.

DISTRIBUTION: Turtle Bay, Baja California to Ancon, Peru.

HABITAT: Sandy surge-beaten beaches; sandy-silt areas adjacent to rivers where water flow is fairly rapid, e.g., Playas del Coco, Costa Rica.

HABITS: Distinguishable from *O. gaudichaudii* by absence of ocular styles. Burrows similar to common mode for *O. gaudichaudii.* Completely nocturnal in habits except when very young (see remarks in discussion of *O. gaudichaudii*). They are scavengers and their rapid movements when disturbed contribute to their common name, ghost crab. Feeding begins shortly after onset of ebb until about mid-flood tide. Activity greatest during ebbing of tide and at slack water.

COMMON NAME: Ghost crab.

REFERENCES: Bott, 1955 (D,T); Crane, 1941b (B); Garth, 1960 (D); Rathbun, 1918 (D,T).

8. *Ocypode quadrata* (Fabricius, 1787)

COLOR: Upper surface white with small black spots or generally a pale yellow or a grayish white or a speckled brown. Many show a degree of iridescence along the outer areas of the carapace. The general color pattern is apparently associated with the color of the substratum of the habitat, e.g., dark brown at Tortuguero, Costa Rica, while pale yellow at Punta Cahuita, Costa Rica. Chace and Hobbs (1969) give a detailed account of the two color phases found on Dominica.

DISTRIBUTION: Atlantic coasts of America. Rhode Island to Estado do Santa Catharina, Brazil, including most of the islands in the greater and lesser Antilles.

HABITAT: Sandy beach areas from upper tidal level to well beyond supralittoral area. Distance from sea generally associated with distribution of same and associated vegetation.

HABITS: Burrows deep, .45-.75 m. Chace and Hobbs (1969) note two types of burrows: 1) vertical or nearly so; and 2) U-shaped. Throughout most of Central America, the U-shaped are most common with the bottom of the U about .45 m. Burrow construction is initiated by a general scratching using the chelipeds followed by removal of sand for the entrance using the dactyli of the walking legs. Once the burrow is sufficiently deep, sand is then transported in either the right or left cheliped to the surface and then dumped, or it may be tossed out of the burrow using either cheliped. These crabs are scavengers and are probably a geminate species of *O. occidentalis* in the Pacific.

COMMON NAME: Ghost crab. (In the past also called a sand crab, but this name is more commonly applied to members of the unrelated genus *Emerita.*)

REFERENCES: Bott, 1955 (D,T); Chace and Hobbs, 1969 (G); Chace

and Holthuis, 1948 (T); Pearse, 1916 (G); Rathbun, 1918 (D,T), 1933 (D,T).

Note: This has until recently been cited by many authors as *O. albicans* Latreille, 1802 (see Chace and Hobbs, 1969).

9. *Ocypode ceratophthalma* (Pallas, 1772)

COLOR: Generally the dorsal appearance is from sage green and yellow to grayish white. Tweedie (1950) gives the color for those found on the Cocos-Keeling Islands as uniform gray, but sometimes olive, and with a splash of yellow on the chelae. The color is highly variable, and associated with the character of the substratum (see Green (1964) for discussion of color changes in Hawaiian forms).

DISTRIBUTION: East coast of Africa (Port St. John), Red Sea, Indo-Pacific North to Kii Peninsula, Japan, including many islands (Mauritius, Maldive and Laccadive Islands, Caroline and Marshall Islands, Tuamotu Islands, Guam and Hawaiian Islands).

HABITAT: Sandy beaches.

HABITS: Burrows are common from the high tide mark to 6-10 m above; less frequently they occur in areas beyond the edge of the sea. They have also been reported along the margins of lagoons. Burrows are generally 37-50 cm deep. In those sites affected by tidal flux the crabs emerge from their burrows during the ebbing of the tide to feed. They are scavengers feeding on debris deposited by the tidal exchange; in the areas above the tidal influence they feed on small organisms, e.g., crickets (Gressitt, 1954). Well defined ocular styles are present in adults of this species.

COMMON NAMES: Ghost crab; Kepiting Mata Panjang (Longeyed crab) (Christmas Island, Indian Ocean).

REFERENCES: Alcock, 1900 (D,T); Barnard, 1950 (D,T); Borradaile, 1902 (B); Dakin et al., 1952 (G); Day et al., 1954 (B,D); George and Knott, 1963 (D,T); Gordon, 1934 (D); Green, 1964 (B); Holthuis, 1953 (D); Miers, 1880 (D); Millard and Harrison, 1954 (G); Sakai, 1940 (D); Tesch, 1918 (D,T); Tweedie, 1950 (D,T); Ward, 1934 (D).

Genus *Uca* Leach, 1814

CHARACTERS: Carapace deep, somewhat broader than long and with antero-lateral area pronounced and/or projected, orbits deep and oblique; antennae large and pronounced; epistome short and distinct; chelipeds of males extraordinarily unequal and large while in female equal and small; ambulatory legs longer than small cheliped of male and both chelipeds of female, last pair of ambulatory legs shorter than rest.

DISTRIBUTION: American Atlantic (Boston to Uruguay), Mediterranean, west coast of Africa (Portugal to Angola), east coast of Africa to Indo-Pacific, including Maury Islands, and eastern Pacific (British Columbia to Valparaiso, Chile).

HABITAT: Associated with a wide variety of mud-sand habitats, e.g., clay tidal flats, salt marshes, mangroves, low tide muddy areas, etc.

HABITS: Most construct well-defined burrows where substratum is moist enough to maintain burrow configuration. Area may be exposed or associated with dense vegetation (e.g., mangroves, *Avicennia*, or pickle weed, *Salicornia*). Many species show a correlation of burrow site with tidal flux whereas others occur widely throughout tidal zone even when burrows may become quite dry. Most species show considerable social behavior. Crane (1941a, 1943b, and 1957) gives a thorough account of display, breeding and relationships of a number of sympatric species of the genus. See Salmon (1965) for an additional account of courtship behavior. There is considerable taxonomic discord associated with this genus due to voids in collections from certain areas and the high degree of variability in color.

REFERENCES: Barnard, 1950 (D,T); Bott, 1954 (D,T); Crane, 1941a (G), b (B), 1943a (D), b (B), 1957 (B); Hagen, 1968 (D); Salmon, 1965 (B); Schmitt, 1921 (D).

10. *Uca pugilator* (Bosc, 1801)

COLOR: Carapace cream white; large cheliped of male buff with apricot at base of movable finger; chelipeds of small males and females white with a grayish cast.

DISTRIBUTION: Boston Harbor, Massachusetts, to Brownsville, Texas.

HABITAT: Sandy areas where sand content is generally more than 40 per cent.

HABITS: They construct well defined, moderately deep burrows showing considerable variation with age and location. See Pearse (1914a) and Dembowski (1925) for details of burrow construction. Feeding, burrow repair-construction and social behavior occur during the low tide period, generally ceasing when the tidal level reaches the burrow entrances; however, some of these events are correlated with sunset and sunrise as well (see Salmon, 1965). This species is restricted by substratum preference. In a typical situation the sand content may increase down a bank from 10 per cent at the top to 60-70 per cent at the low tide level, with the crabs feeding at the lower levels and living near the top. See Teal (1958) for an account of feeding habits as related to sand content.

COMMON NAME: Sand fiddler crab.

REFERENCES: Burkenroad, 1947 (B); Crane, 1943b (B); Dembowski, 1925 (B); Pearse, 1914a (B), b (B); Salmon, 1965 (B); Salmon and Stout, 1962 (B); Teal, 1958 (B).

11. *Uca subcylindrica* (Stimpson, 1859)

COLOR: No record.

DISTRIBUTION: Corpus Christi, Texas to northern Mexico.

HABITAT: Mud-sandy areas in and adjacent to estuarine situations.

HABITS: Burrows are small, slightly twisted, and constructed in loose sandy soil with high moisture content or in muddy areas. Burrows seldom deeper than .75 m. Little other ecological data recorded for this species.

COMMON NAME: Puffed fiddler crab.

REFERENCE: Rathbun, 1918 (D,T).

12. *Uca tangeri* (Eydoux, 1835)

COLOR: Carapace reddish brown to dirty yellow; male large cheliped reddish brown to pale blue; female chelae dirty cream with some pinkish areas.

DISTRIBUTION: Portugal, north and west coasts of Africa to Angola.

HABITAT: Sandy areas adjacent to brackish water; salt marshes; not common on open coasts.

HABITS: Burrows which extend downward for about 30 cm or so are located from the mean tide to highest high tide level. The top of the burrow is generally plugged with 7.5-10 cm of excavated substratum by the time the burrow is covered by the tide. As the tide recedes the plug is removed and the crab emerges to feed, etc. Habits vary from solitary to colonial. In colonial situations, e.g., salt marsh flats, the burrows are still simple, but they often intersect. See Hagen (1961) and Hediger (1934) for additional details.

COMMON NAMES: Fiddler crab; Calling crab.

REFERENCES: Altevogt, 1959 (B), 1962 (B); Barnard, 1950 (D,T); Hagen, 1961 (D), 1962 (B); Hediger, 1933 (B), 1934 (B); Rathbun, 1921 (D,T).

Note: This was described by Eydoux in 1835 as *Gelasimus tangeri*, and is recorded as such by some authors.

Genus *Ucides* Rathbun, 1897

CHARACTERS: Interorbital distance a little more than one-half the greatest width of the carapace; orbits deep but not much larger than the eyes; antennules oblique; epistome small but prominent; legs stout.

DISTRIBUTION: East and west coasts of the Americas.

HABITAT: Common inhabitants of muddy shores and mangrove swamps where there is a moderate degree of tidal flux.

HABITS: Burrows constructed below the highest high tide level most commonly at midtide level so that burrows covered daily by tidal surge. Burrows not uniform, generally shallow, relatively straight, and frequently with multiple entrances; almost always filled with ground water to the level of the burrow mouth. Juveniles occur in dense numbers per unit area within an interchange of intersecting burrows or in burrows of less density per unit area but where the burrow is directly adjacent and/or attached to those of adults.

REFERENCES: Bright, 1966 (G); Rathbun, 1918 (D,T).

Note: Until recently this genus was placed among the members of the family Gecarcinidae but Chace and Hobbs (1969) placed it among the members of the family Ocypodidae.

13. *Ucides cordatus* (Linnaeus, 1763)

COLOR: Carapace pale yellow with cervical groove and urogastric lobe rusty brown; walking legs red-violet; tips of chelae cream. Young with a tendency to have a dark gray area along the median anterior margin of the carapace. Color is variable throughout the range of distribution primarily associated with the nature of the habitat substratum.

DISTRIBUTION: Atlantic coasts of America. Southern Florida (Biscayne Bay) to Santos, Brazil, including the West Indies.

HABITAT: Areas, frequently flooded by tidal surge, in mangroves along mouths of rivers and brackish water marshes adjacent to the sea.

HABITS: This crab constructs burrows in very soft mud in areas where there is an absence of low ground vegetation (shrubs). Primary sites are mangroves with burrows concentrated along the upper edge of distribution of the red mangrove (*Rhizophora mangle*). Burrows are wide, mostly straight and relatively shallow. Young and adults construct their burrows in close proximity. At both ends of the range there is some indication that burrows are shallower and often nothing more than depressions. This is a twin species of *U. occidentalis* in the Pacific.

COMMON NAMES: Pagurus; Kaburi (Cuba); Uçá (Brazil).

REFERENCES: Bott, 1955 (D,T); Bright, 1966 (G); Chace and Hobbs, 1969 (G); Garth, 1960 (D); Manning and Provenzano, 1961 (D); de Oliveira, 1946 (B); Rathbun, 1918 (D,T), 1933 (D,T).

14. *Ucides occidentalis* (Ortmann, 1897)

COLOR: Carapace reddish gray with orange-red on the lateral margin; however, older forms tend to become rust red due to staining from the mud in the burrow. The last three ambulatory legs and most of the chelipeds dark red; dactyli of chelipeds reddish white; underside brownish white. Molt condition not predictable from color change.

DISTRIBUTION: Pacific coast of America (Espíritu Santo Island, Baja California to Rio Tumbes, Peru).

HABITAT: Mud of mangrove areas, mouths of rivers and brackish water marshes.

HABITS: This species maintains burrows in areas which are generally covered by high tide at least once per month. Burrows are most common along the mud-water margin of mangroves; may be associated with salt marsh vegetation, e.g., *Salicornia, Sueda*, etc. Burrows are shallow and often with more than one entrance. Typically, there is a small side chamber or tunnel paralleling the surface just inside the mouth of the burrow. Juveniles are most often found in small pockets connecting to the burrows occupied by the adults. Burrows do not generally extend more than 50 cm below the surface. This is a geminate species of *U. cordatus* which occurs in the Atlantic.

COMMON NAMES: Wide red land crab, Cangrejo amarillo (Peru).

REFERENCES: Bright, 1966 (G); Garth, 1960 (D); Rathbun, 1918 (D,T).

Family GECARCINIDAE

Genus *Gecarcoidea* Milne Edwards, 1837

CHARACTERS: Fronto-orbital border less than half the greatest breadth of carapace; orbits deep; antennae very small and excluded from the orbit; epistome sunken and quite hairy; chelipeds equal or nearly so in both sexes; legs stout.

DISTRIBUTION: Indo-Pacific Islands.

HABITAT: Moist soil or muddy areas in the jungle areas adjacent to the sea.

HABITS: Burrows shallow and not well developed.

REFERENCES: Calman, 1911 (B); Gibson-Hill, 1947 (B); Keilin, 1921 (D); Rathbun, 1918 (D,T); Tweedie, 1947 (D,T); Webb, 1922 (B).

15. *Gecarcoidea humei* (Wood-Mason, 1873)

COLOR: Dorsal surface a relatively uniform red-violet with some indication of red near the base of the chelae; claws white-brown with reddish violet tinge; scars on carapace yellow or yellowish white.

DISTRIBUTION: Indo-Pacific Islands (Nicobars, Andamans, New Britain, Celebes, Christmas (Indian Ocean), Philippines, Loyalties, Formosa, New Guinea, Pulu Weh, and Talauts.

HABITAT: Moist areas along the coasts of islands, typically within the jungle.

HABITS: Burrows not well developed; generally shallow 15-60 cm in length; mostly parallel with the surface; burrows principally for retreat. Found only where there is a constant source of water to keep soil moist. Andrews (1900) gives a good account of selected aspects of the life history of this species. Gibson-Hill (1947) reports extensive migrations to the sea during spawning together with an account of the aspects of development of the young.

COMMON NAME: None recorded.

REFERENCES: Andrews, 1900 (B); Calman, 1909 (B); A. Milne Edwards, 1879 (T); H. Milne Edwards, 1834 (T), 1837 (T); Ortmann, 1894 (D,T); Pocock, 1888 (D); Rathbun, 1918 (D,T); Sakai, 1940 (D); Tweedie, 1947 (D,T), 1954 (B); Wood-Mason, 1873 (T).

Note: This is frequently listed as *Gecarcoidea lalandii* H. Milne Edwards, 1837. The genus was erected by H. Milne Edwards (1837) for *G. lalandii* which was erroneously recorded from Brazil, and then renamed by the same author in 1853 as the genus *Pelocarcinus*. Wood-Mason (1873), de Man (1879), and Pocock (1888) all described this under a number of genera and species. Ortmann (1890) reduced all these species to synonymy with *Gecarcoidea lalandii* except Pocock's *natalis*. Tweedie (1947) gives a good review of this taxonomic snarl and concludes that *G. lalandii* must

be regarded as indeterminable on the basis of an incorrect type locality. We use the name *humei* on the advice of Wood-Mason (1873). Tweedie (1947) also supports the position that because these are generally island forms there are several variants which can be recognized as subspecies, e.g., the crab found on Christmas Island (Indian Ocean) is *G. humei natalis* (Pocock).

Genus *Cardisoma* Latreille, 1825

CHARACTERS: Fronto-orbital distance much more than half the greatest width of the carapace; orbits deep with eyes filling half of the orbit; antennules folded; epistome short and well defined; legs stout.

DISTRIBUTION: Tropical America, Cape Verde Islands, west coast of Africa, Indo-Pacific from Port St. Johns, Africa to Hawaiian Islands.

HABITAT: Commonly inhabits muddy shores, mangrove swamps and saline lowland soils near the coast.

HABITS: Constructs well defined deep burrows in soft soils where ground water is available during the dry season. Often they plug the burrow mouth with mud during the dry season to keep the lower portions of the burrow moist. Burrow sites are always above the mean high tide level. They return to the sea to spawn and to introduce the pre-zoea to the required sea water environment. All are primarily herbivorous but feed on carrion also.

REFERENCES: Barnard 1950 (D,T); Behre, 1949 (B); Bright, 1966 (G); Gifford, 1963 (G); Herreid and Gifford, 1963 (B); Holthuis, 1959 (D); Rathbun, 1918 (D,T); Tesch, 1918 (D,T).

16. *Cardisoma guanhumi* Latreille, 1825

COLOR: Carapace deep violet in young, but tends to become bluish gray with age or approach to molt; ambulatory legs deep blue with larger cheliped dirty white. Local variation may be due to the type of soil characteristic of habitat.

DISTRIBUTION: Atlantic coasts of America, central east coast of Florida, Louisiana, Texas to Florianópolis, Brazil, including the West Indies.

HABITAT: Open fields, margins of mangrove swamps, along margins of rivers, in forests, along roads and under houses. In all known situations the soil is saline.

HABITS: All are typically found within a few hundred yards of a brackish or saltwater source. The young are found under debris, e.g., coconut husks, palm fronds, flotsum, etc., directly adjacent to salt water (generally above the highest high tide level) or in the burrows of adults. Adults construct burrows of varying depth and structural complexity, depending upon their age and the location of the burrow with respect to available ground water. Large aggregations of adult crabs are often found in areas where the substratum is soft yet still suitable for burrows, and where there is little ground cover. Although adults occur several hundred meters from the sea, they are most common within about 200 meters of the tidal zone. Inland dwelling

individuals migrate to the sea in great numbers during the breeding season to shed their eggs. This is a twin species of *C. crassum* which occurs in the Pacific.

COMMON NAMES: Great land crab; White land crab, Juey, Cangrejo; Guanhumi; Mulatto land crab; Guaiamú, guaraní, guayamu (Brazil).

REFERENCES: Behre, 1949 (B); Bott, 1955 (D,T); Bright, 1966 (G); Chace and Holthuis, 1948 (T); Feliciano, 1962 (B); Gifford, 1963 (G); Herreid, 1963 (B), 1967 (B); Herreid and Gifford, 1963 (B); de Oliveira, 1946 (B); Pearse, 1916 (G); Peyton et al., 1964 (D); Rathbun, 1933 (D,T).

17. *Cardisoma crassum* Smith, 1870

COLOR: Carapace deep blue; dactyli of walking legs red; large cheliped pale yellow to dirty white; underside cream-white.

DISTRIBUTION: Pacific coasts of America. Todos Santos, Baja California to the Rio Chira, Peru.

HABITAT: Open fields, margins of mangrove swamps, along roads and fence-rows, margins of rivers and streams, under houses and in cultivated fields; generally in saline lowland soils near the coast.

HABITS: These show habits similar to those of *C. guanhumi* in areas adjacent to brackish or salt water sources. In contrast to *C. guanhumi* the young construct separate shallow burrows along river banks and edges of mangroves. Adult burrow construction parallels that of *C. guanhumi.* During the dry season, adults with burrows in open, exposed areas close the top of the burrow with a plug of mud. Some reports have indicated that closure of the burrow also occurs prior to the onset of ecdysis (shedding). Adult migrations to the sea during the spawning period are common in Mexico, Costa Rica, Panama, and Ecuador. This is a geminate species of *C. guanhumi* which occurs in the Atlantic.

COMMON NAMES: Mouthless crab, Cangrejo sin boca (Peru), Cajo (Mexico).

REFERENCES: Bott, 1955 (D,T); Bright, 1966 (G); Garth, 1948 (D,T), 1960 (D); Murphy, 1944; Pesta, 1931 (D,T); Rathbun, 1918 (D,T).

18. *Cardisoma armatum* Herklots, 1851

COLOR: Young, newly molted individuals with violaceous carapace; tips of chelae and walking legs bright red; with age and approach to molt carapace turns dirty yellow with occasionally slight reddish spots dorsally.

DISTRIBUTION: Western coast of Africa from St. Louis to Baia dos Tigres, Angola, Africa and Cape Verde Islands.

HABITAT: Moist sandy areas above the mean high tide level; mangroves, mouth of rivers, under houses, in cultivated areas adjacent to permanent sources of brackish or sea water; and inland areas of larger islands.

HABITS: Youngest juveniles are in small depressions or newly dug shallow burrows directly adjacent to water; older juveniles found in smaller compartments within the burrows of adults. Adults construct deep burrows,

and often these are part of a large colony where the burrows intersect. Both juveniles and adults are nocturnal scavengers, often moving considerable distance from their burrows to feed on palmnuts, coconuts, dead fish and scraps of vegetation. Spawning activities have not been recorded in the literature for this species.

COMMON NAME: Edible land crab.

REFERENCES: Barnard, 1950 (D,T); Cheesman, 1922 (B), 1923 (B); Dalziel, 1920 (D); Rathbun, 1921 (D,T); Wanson, 1935 (D).

19. *Cardisoma carnifex* (Herbst, 1794)

COLOR: Carapace dark purple; chelipeds light purple to dark cream.

DISTRIBUTION: East coast of Africa, whole of Indo-Pacific, north eastern Australia and north toward Japanese Mainland (Loo Choo), including Mauritius, Madagascar, Andaman Islands, Malay Archipelago, Polynesia and Melanesia.

HABITAT: Common inhabitants of muddy shores, mangrove swamps or Kuli and saline lowland soils near the coast. Not uncommon in the jungle adjacent to the sea. All around the Indian Ocean it is most commonly found between the high tide mark and just beyond the extreme highest high tide line.

HABITS: Constructs well defined burrows in soft soils where ground water is available during the dry season. Habits generally parallel other members of the genus. On coral atolls it is common among coconut husks, under rubble piles and in mixed forest areas adjacent to plantations.

COMMON NAMES: Land crab; Kepiting Balong (Cocos Island), Papaka Tupa (Tuamotu Islands).

REFERENCES: Alcock, 1900 (D,T); Barnard, 1950 (D,T); Borradaile, 1902 (B); Forest and Guinot, 1961 (D); Hogue and Bright, 1971 (B); Holthuis, 1953 (D); Macnae, 1963 (B,D), 1966 (B,D); Miyake, 1939 (D,T); Silas and Sankarankutty, 1960 (B); Stebbing, 1910 (D); Tesch, 1918 (D,T); Tweedie, 1950 (D,T).

Note: Over much of the range this occurs in sympatry with *C. hirtipes* (see Miyake, 1939).

20. *Cardisoma hirtipes* Dana, 1851

COLOR: Carapace generally dark violet and chelae bright cinnamon red. There is considerable color variation throughout the Indo-Pacific, e.g., Tweedie (1947) notes that on Christmas Island (Indian Ocean) the carapace is light bluish gray and the chelae are dirty white.

DISTRIBUTION: Occurs in sympatry with *C. carnifex* from east coast of Africa throughout whole of Indo-Pacific. Miyake (1939) gives a good account of the distinguishing species characteristics.

HABITAT: Moist saline soils; mud banks in the immediate neighborhood of fresh-water. Where soil is dense or crusted they frequently scratch-out a space under a treeroot or rock.

HABITS: Normally the crab digs burrows in the soft mud directly adjacent to streams. The burrows are only 50-75 cm below ground level. Considering our preliminary studies on related species it seems likely that this species can abide in areas where there is more ground water than is characteristic for *C. carnifex*. Perhaps it is the ecological equivalent of the American species of the genus *Ucides*. A few weeks after the onset of the rainy season in January or February spawning occurs. Copulation occurs at the edge of the sea just prior to the time the female sheds the previous batch of eggs. They are primarily plant feeders, occasionally causing crop damage to melons and pumpkins (Esaki, 1940), but in areas associated with human habitation they are carrion feeders as well.

COMMON NAME: Land crab.

REFERENCES: Alcock, 1900 (D,T); Esaki, 1940 (D); Gibson-Hill, 1947 (B); Gordon, 1934 (D); Miyake, 1939 (D,T); Sakai, 1940 (D); Tesch, 1918 (D,T); Tweedie, 1947 (D,T).

Note: Tweedie (1950) restored *Cardisoma frontalis* H. Milne Edwards, 1853, to specific status from synonymy with *Cardisoma hirtipes*. He gives the distribution of *C. frontalis* as Loyalty Islands, northern Daitozima, Japan, and Cocos-Keeling Islands, and further states that examination of series presently considered as *C. hirtipes* would probably result in extension of this distribution. However, until there is an extensive revision of the genus with clarification of the number of island endemics we will herein consider these still to be *C. hirtipes*.

Genus *Gecarcinus* Leach, 1814

CHARACTERS: Fronto-orbital distance half or less than half of the greatest width of the carapace; orbits deep with eyes nearly filling the orbits; antennae very short; epistome linear; legs stout, the second pair being longest.

DISTRIBUTION: Tropical America, Bermudas, Ascension Island, West and South Africa, Australasia.

HABITAT: Drier areas above the tidal margins of mangroves; river mouths and adjacent coastal sandy and saline soil areas.

HABITS: Burrows always shallow and devoid of ground water, except during rain storms. Many utilize debris as a source of protection in lieu of a burrow. In the extreme northern and southern portions of the distribution the burrows are deep 1.2 m and often with mouth plugged during the dry season.

REFERENCES: Bright, 1966 (G); Finnegan, 1931 (D); Garth, 1948 (D,T); Chace and Hobbs, 1969 (G); Villalobos and Cabrera, 1964 (B).

21. *Gecarcinus planatus* Stimpson, 1860

COLOR: Body and legs generally an orange-red; tips of walking legs often dark red; tips of chelae cream with small flecks of brown.

DISTRIBUTION: Pacific coasts of America. Restricted to islands from west coast of Mexico to Colombia.

HABITAT: Rocky areas, under roots and in soft soils above highest high tide mark on slopes up to 120 m, often associated with beach strand vegetation.

HABITS: Adults and older juveniles scratch out shallow burrows under rocks, roots or debris. Burrow serves primarily as a hiding place. Young hide in natural crevices and small spaces providing natural protection. Burrows have no standing water. Newly metamorphosed juveniles hide along the shore under debris, often gregariously. They are nocturnal feeders, and commonly move considerable distance from their burrows. Bold when on feeding excursions, ambling over almost anything in their path, e.g., sleeping scientists, food lockers, young birds, etc. This is a geminate species of *G. ruricola* occurring in the Atlantic.

COMMON NAMES: Island crab; Big red crab; Cangrejo rojo (Panama).

REFERENCES: Garth, 1948 (D,T), 1960 (D); Rathbun, 1918 (D,T).

22. *Gecarcinus ruricola* (Linnaeus, 1758)

COLOR: Body and legs generally black with purplish tinge; small light yellowish spot on the posterior margin of the carapace; last two joints of legs red; red and yellow patch below the orbit of the eye; abdomen light yellow with violet hue; older individuals or those undergoing late preecdysial changes are overall much lighter in color.

DISTRIBUTION: Atlantic coasts of America. Restricted to islands: Bahamas; southern Florida; greater and lesser Antilles; Curaçao, and Cayman Islands.

HABITAT: Low and marshy areas not far from the sea; lower slopes of island mountains up to 500 meters.

HABITS: They hollow out obliquely inclined shallow burrows, which are quite frequently under a tree or the edge of a large rock. After metamorphosis, the young are found in large numbers just above the high tide level, however, very shortly after the second or third molt they move to areas well above the highest high tide. Along the shore edge, they are often found sympatrically with *Gecarcinus lateralis.* On larger islands, e.g., Isla Providencia, Colombia, they are common along mountain slopes and cliffs adjacent to the beach and to heights of 500 meters and as far as a thousand meters from the shore. They are more secretive than most of the gecarcinids. During the rainy season they are reported to move in large numbers to the sea to breed. This is a geminate species of *G. planatus* in the Pacific.

COMMON NAMES: Black crab; Mountain crab; Blue land-crab, Red tourlourou.

REFERENCES: Chace and Hobbs, 1969 (G); Chace and Holthuis, 1948 (T); Rathbun, 1918 (D,T).

23. *Gecarcinus quadratus* Saussure, 1853

COLOR: Carapace brownish red with two white spots in the cardiac region, intestinal region orange-red; large chelipeds with light purple tinge;

merus of maxilliped light yellow; underside sooty white.

DISTRIBUTION: Primarily Pacific coasts of America. (Atlantic side of Colombia). Not known to occur on permanently isolated islands. Acapulco, Mexico to La Libertad, Ecuador; Turbo.

HABITAT: Above the highest tide zones of sandy beaches in moist forest and mangrove areas where there is low growing vegetation or debris.

HABITS: All occur in drier areas directly adjacent to mangroves or the ocean. They are most common along the uppermost areas of sandy beaches from 1.5 - 15 m above the supratidal area where there is a dense covering of debris, e.g., coconut husks and fronds, or low growing beach strand vegetation, e.g., *Ipomoea* (family Convolvulaceae). Burrow construction is correlated with the length of the dry season. Crabs at both extremes of the distribution tend to construct simple burrows, 7-50 cm deep, while at mid-range, burrows are not common. Non-burrowers tend to occupy small depressions under vegetation debris, houses, etc. This is a geminate species of *G. lateralis* in the Atlantic.

COMMON NAMES: Red land crab; Whitespot crab.

REFERENCES: Bright, 1966 (G); Finnegan, 1931 (D); Garth, 1948 (D,T); Pesta, 1931 (D,T).

24. *Gecarcinus lateralis* (Freminville, 1835)

COLOR: Carapace dark red with small white spots just posterior to the eyes and a pair of white spots in the cardiac region; underside cream-white; chelipeds reddish gray; dactyli sooty gray. Pattern of dark red carapace highly variable throughout range of distribution and in distinct (isolated) populations.

DISTRIBUTION: Atlantic coasts of America. Bahamas; Florida Keys; South Padre Island, Texas; Yucatan; to Macuto, Venezuela. Also occurs on islands in the West Indies.

HABITAT: Along the upper dry zone of sandy beaches and adjacent low hills, 6 to 9 m above highest high tide level; associated with a variety of beach strand vegetation, e.g., coconuts, and low growing vines, e.g., *Ipomoea*.

HABITS: All occur in nearly dry areas, i.e., where there is no standing water but a good bit of interstitial soil moisture. Burrow construction is as for *G. quadratus*. There is also a tendency for the depth of the burrow to be correlated with the length of the dry season. Burrows are deeper on the extremes of the range of distribution.

COMMON NAMES: Black land-crab; Common land-crab.

REFERENCES: Bliss, 1964 (B); Bott, 1955 (D,T); Bright, 1966 (G); Cabrera, 1965 (B); Chace and Hobbs 1969 (G); Chace and Holthuis, 1948 (T); Pearse, 1916 (G); Rathbun, 1918 (D,T), 1933 (D,T); Ray, 1967 (D).

ARTHROPOD INHABITANTS OF LAND CRAB BURROWS

The following list represents an attempt to cite all published records of arthropods found in land crab burrows. Because the host was not identi-

fied in all cases and there is frequent confusion in usage of the terms land crab, crab, lobster, mud lobster, crayfish, etc., references to all are included. Accounts of dubious validity are also included for completeness and to establish the need for verification.

Some explanation is in order regarding certain assumptions made and conventions used in compiling the list. 1) Identifications and associations with the host crab, i.e., the determinations of the real crab owner of the burrow from which the associates were collected, are assumed to be correct. The list has been read by various specialists and it is hoped that errors of identification, erroneous records and synonymies have been largely detected. 2) The type of association and degree of dependence (see Table I and discussion of the Crabhole Community above) of the species on the crabhole were ascertained or inferred from all available information on the biology of the species. Dubious decisions and the criteria for allocation to a category are explained where relevant.

INSECTS

Order DIPTERA

Family CULICIDAE

We found it impossible to scour the voluminous literature on mosquitoes for all records of species utilizing crabholes. Fortunately, for most regions, comprehensive (though not always current) reviews including ecological data are available (Belkin, 1962: South Pacific; Steffan, 1966: Papuan Region; Hopkins, 1952: Ethiopian Region; Dyar, 1928: tropical America; Delfinado, 1966: Philippines; Barraud, 1934: India; Mattingly, 1958, 1959: Indomalayan Region).

Presently 140 species of mosquitoes are recorded as either resting as adults or breeding in crabholes. To this list could be added several more from unpublished works known to us and no doubt others from other studies now under way. Surprisingly no culicidologist has attempted previously an exclusive investigation of this habitat. Most authors, with a few notable exceptions, seem to regard the crabhole as an aberrant breeding site being utilized by only a handful of specially adapted species. Our bibliographic research would indicate that, whereas those taxa specifically adapted to crabholes are indeed few, the number of transient species is much larger than previously suspected. We feel that much more attention should be paid to crabholes in general mosquito surveys than has been customary in the past (see remarks of Peyton, 1970:2-3). Crabholes are easily sampled using the crabhole pump and collection methods described by Belkin et al. (1965: 37-38).

Most of these transient crabhole breeders are salt water adapted or tolerant species which are general ground pool breeders along the coast.

Their usual normal habitats consist of salt marshes, mangrove pot holes, tidal pools, puddles, coral rock pools, etc. A considerable number of container breeding species (tree holes, especially in mangroves, and artificial containers) also are found in the crabhole. From this it seems probable that the specific crabhole mosquito fauna is of mixed origin derived from both of these more primitive categories through convergent adaptations (van den Assem, 1961:19).

The nature of these adaptations is virtually unstudied. Some characteristics frequently observed in crabhole species are as follows: 1. Stubby or vestigial anal papillae on the larvae. This condition is common, but by no means universal, among larvae which develop in waters with high salt content. 2. Short head hair 1-C, the adaptive significance of which is totally obscure. 3. Prolonged developmental period. 4. Very specialized and aberrant reproductive behavior such as pupal attendance and lack of swarming in *Deinocerites* (Provost and Haeger, 1967) and oviposition directly on the host crab in *Aedes pembaensis* (Goiny et al., 1957).

At least a few crabhole mosquitoes are of known public health importance. Two primary vectors of serious diseases in Africa, while not specific or even semispecific members of the crabhole community, nevertheless may develop in tremendous numbers in this habitat and may even find refuge there during eradication programs designed to treat only the more usual breeding sites. These species are *Aedes aegypti* and *Anopheles gambiae* (? *melas, merus*) for both of which there are several well authenticated records of breeding in crabholes (see list). Vectors of filariasis on the east African coast, *Aedes pembaensis*, and in the south Pacific, *Aedes polynesiensis*, are semispecific members of the crabhole community. The former species has also been found to harbor several kinds of viruses of unknown but possible pathogenicity (Heisch et al., 1956), as have various other mosquitoes which develop in crabholes, including *Deinocerites*. The eastern Equine, Venezuelan and St. Louis encephalitis viruses have all recently been isolated from *D. pseudes* in Panama (Galindo, 1967; Templis and Galindo, 1970:175; Grayson, 1967). Trypanosome organisms have also been recently isolated from wild adults of this species in Panama (Gorgas Mem. Lab., 1970). While *Deinocerites* do not appear to be strongly anthropophilic they may act as important agents in maintaining virus reservoirs in coastal animal populations (silent cycles) and which may enter the human population via other vectors.

Genus *Aedes*

Subgenus *Aedimorphus*

A. abnormalis (Theobald, 1910)

DISTRIBUTION: Tropical Africa; interior and coastal.
CRAB HOST: *Cardisoma armatum*.

TYPE: Transient. Adults only. Probably breeds in ground and rock pools.

REFERENCE[1]: Wanson, 1935:576.

A. albocephalus (Theobald, 1903)

DISTRIBUTION: Tropical Africa, Madagascar, Seychelles; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Accidental. Normally breeds in grassy swamps, pools, etc., in interior; saline seepage pools on coast.

REFERENCES: Hopkins, 1952:182; Ingram and Macfie, 1917:142 (and as *minutus*).

A. caliginosus (Graham, 1910)

DISTRIBUTION: Nigeria; coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Adults only. Recorded also from borrow pits and stream pools.

REFERENCE: Dalziel, 1920:253.

Note: Identification dubious.

A. centropunctatus Theobald, 1913

DISTRIBUTION: Sudan, British West Africa; interior by watercourses (?).

CRAB HOST: *Sudanonautes africanus.*

TYPE: ? Bionomics insufficiently known.

REFERENCE: Hanney, 1960:99.

A. domesticus (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in grassy swamps, borrow pits, etc.

REFERENCE: Wanson, 1935:576-577, 579.

A. durbanensis (Theobald, 1903)

DISTRIBUTION: Africa, Arabia; primarily coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in fresh water ground pools.

REFERENCE: Wanson, 1935:576-578.

A. fowleri (Charmoy, 1908)

DISTRIBUTION: Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

[1]Unless followed by symbols indicating additional significant information (T–taxonomy; B–biology; D–distribution; G–general), the references cite only records of the occurrence of the species in crabholes.

TYPE: Transient. Usually breeds in rock pools and grassy ground pools.
REFERENCE: Wanson, 1935:576-577, 579 (as *nigeriensis*).

A. irritans (Theobald, 1901)

DISTRIBUTION: West and Central Africa; primarily coastal.
CRAB HOST: *Cardisoma armatum.*
TYPE: Semispecific. Breeds also in small brackish pools along the coast. Strongly anthropophilic.
REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119-120 (B); Dalziel, 1920:251-253; Dunn, 1928:249; Ingram & Macfie, 1917:135; Kumm, 1931:65; Wanson, 1935.

A. nigricephalus (Theobald, 1901)

DISTRIBUTION: West Africa; coastal.
CRAB HOST: *Cardisoma armatum.*
TYPE: Semispecific. Also breeds in ground pools.
REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920: 251; Dunn, 1928:249; Kumm, 1931:65; Wanson, 1935.

A. punctothoracis (Theobald, 1910)

DISTRIBUTION: West tropical Africa; primarily coastal.
CRAB HOST: *Cardisoma armatum.*
TYPE: Accidental. Adults only. Normally breeds only in ground pools.
REFERENCES: Dalziel, 1920:253; Wanson, 1935:576.

A. tarsalis (Newstead, 1907)

DISTRIBUTION: Tropical Africa; interior and coastal.
CRAB HOST: *Cardisoma armatum.*
TYPE: Transient. Usually breeds in rock and ground pools.
REFERENCES: Kumm, 1931:65 (as *sudanensis*); Macfie and Ingram, 1916:7 (as *sudanensis*); Wanson, 1935:576-577.
Note: May be confused with *centropunctatus.*

Subgenus *Cancraedes*

GENERAL REFERENCE: Mattingly, 1958.

All species for which the immatures are known (*) are found breeding primarily in crabholes from which all have been taken as adults. The entire subgenus appears to be adapted to this habitat and comprises a specific or semispecific member of the crabhole community though mangrove pot holes and coastal ground pools may serve as secondary breeding sites. All species have a coastal distribution or are found on small islands. None of the crab hosts has been identified.

A. cancricomes Edwards, 1922

DISTRIBUTION: Andaman Islands.

**A. curtipes* Edwards, 1915

DISTRIBUTION: Borneo, Philippines, Malaya, ? Thailand.

*A. *indonesiae* Mattingly, 1958

DISTRIBUTION: Java, Sumatra, east Gulf of Siam.

A. kohkutensis Mattingly, 1958

DISTRIBUTION: Thailand.

A. mamoedjoensis Mattingly, 1958

DISTRIBUTION: Celebes.

**A. masculinus* Mattingly, 1958

DISTRIBUTION: Malaya, ? Philippines.

A. palawanicus Mattingly, 1958

DISTRIBUTION: Philippines.

A. penghuensis Lien, 1968

DISTRIBUTION: Taiwan.

A. simplex (Theobald, 1903)

DISTRIBUTION: Ceylon.

A. thurmanae Mattingly, 1958

DISTRIBUTION: Celebes.

Subgenus *Geoskusea*

GENERAL REFERENCES: Mattingly, 1959; Belkin, 1962:332-339.

As with the preceding, crabholes in coastal areas are the primary breeding places of all species in this subgenus for which the immatures are known (*); the adults of all species have been taken from this habitat. Thus all can probably be classified as specific or semispecific members of the crabhole community. None of the crab hosts has been identified.

A. baisasi Knight and Hull, 1951

DISTRIBUTION: Philippines.

A. becki Belkin, 1962

DISTRIBUTION: Solomons.

**A. daggyi* Stone and Bohart, 1944

DISTRIBUTION: New Hebrides, Solomons.

A. daliensis (Taylor, 1916)

DISTRIBUTION: Australia.

A. fimbripes Edwards, 1924

DISTRIBUTION: Bismark Archipelago, New Guinea.

**A. kabaenensis* Brug, 1939

DISTRIBUTION: Celebes.

**A. longiforceps* Edwards, 1929

DISTRIBUTION: Solomons.

Note: Adults have been observed feeding on mud skippers (*Periophthalmus musgravei*) resting on mangrove roots in the Solomon Islands (Sloof and Marks, 1965).

A. perryi Belkin, 1962

DISTRIBUTION: Solomons.

A. tonsus Edwards, 1924

DISTRIBUTION: Moluccas.

Subgenus *Howardina*

A. inaequalis (Grabham, 1907)

DISTRIBUTION: Jamaica; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Most commonly breeds in treeholes and broken bamboo.

REFERENCE: Berlin, 1969:48.

A. walkeri Theobald, 1901

DISTRIBUTION: Jamaica, interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Normally breeds in bromeliads.

REFERENCE: Berlin, 1969:35.

Subgenus *Levua*

A. suvae Stone and Bohart, 1944

DISTRIBUTION: Fiji; coastal.

CRAB HOST: Not recorded, "crab and lobster holes."

TYPE: Specific. No other recorded breeding site.

REFERENCES: Amos, 1944:32; Belkin, 1962:400 (G).

Subgenus *Mucidus*

A. aurantius chrysogaster (Taylor, 1927)

DISTRIBUTION: Australia, New Guinea; coastal.

CRAB HOST: Not recorded, "crab pot hole."

TYPE: Transient. Usually breeds in various types of ground pools in coastal areas. Larva predaceous.

REFERENCE: Steffan, 1966:206.

A. scatophagoides (Theobald, 1901)

DISTRIBUTION: India, Ceylon, Burma, China, tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in transient ground pools and marshes. Larva predaceous.

REFERENCE: Wanson, 1935:576-577, 579.

Subgenus *Neomacleaya*

A. dux Dyar and Shannon, 1925

DISTRIBUTION: Southeast Asia; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. Usually breeds in puddles and hoof prints near the coast; prefers saline water?

REFERENCE: Delfinado, 1967:20.

A. panayensis Ludlow, 1914

DISTRIBUTION: Philippines, Moluccas, New Guinea; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. Usually breeds in marine littoral ground pools.

REFERENCES: Delfinado, 1968:33; Steffan, 1966:214.

Subgenus *Neomelanoconion*

A. lineatopennis (Ludlow, 1905)

DISTRIBUTION: Oriental Region, tropical Africa, Australia; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. Breeds usually in vegetated ground pools.

REFERENCE: Wanson, 1935:576.

Subgenus *Ochlerotatus*

A. perventor Cerqueira and Costa, 1946

DISTRIBUTION: Brazil; interior and coastal.

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Probably transient. Bionomics poorly known. Only breeding records from crabholes.

REFERENCES: Forattini, 1958: 177-178; Forattini et al., 1958:37 (B).

A. taeniorhynchus (Wiedemann, 1821)

DISTRIBUTION: American coasts and interior saline areas.

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Transient. Salt water breeder, usually found in coastal salt marshes, tide pools, etc., and inland saline sinks. Strongly anthropophilic.

REFERENCES: Belkin et al., 1970:49 (G); Forattini, 1958:175-177 (B); Lutz, 1912:19 (as *Culex taeniorhynchus*) (B); Montchadsky and Garcia, 1966:42; de Oliveira, 1946:297.

Subgenus *Paraedes*

A. bonnae Mattingly, 1958

DISTRIBUTION: Malaya; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in ground pools (palm fronds also recorded).

REFERENCE: Mattingly, 1958:34.

Subgenus *Pseudarmigeres*

A. albomarginatus (Newstead, 1907)

DISTRIBUTION: Central tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: ? Single breeding record, from crabhole.

REFERENCE: Wanson, 1935:577.

Subgenus *Pseudoskusea*

A. lunulatus King and Hoogstraal, 1946

DISTRIBUTION: New Guinea; coastal.

CRAB HOST: Not recorded, "crayfish hole."

TYPE: ? Single breeding record, from crayfish hole in shaded rain forest, 250 feet elevation.

REFERENCE: King and Hoogstraal, 1946a:97.

Subgenus *Rhinoskusea*

A. longirostris (Leicester, 1908)

DISTRIBUTION: Indomalayan, north Australian and Papuan Regions; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in numerous other marine littoral ground pool habitats, especially mangrove swamp pools, and artificial containers.

REFERENCES: Colless, 1957:144; Leicester, 1908:8 (as *Ficalbia longirostris*); Mattingly, 1958:39-40.

A. pillaii Mattingly, 1958

DISTRIBUTION: Malaya; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in numerous other marine littoral ground pool habitats.

REFERENCE: Reid *in litt.* after Mattingly, 1958:40.

Subgenus *Skusea*

A. pembaensis Theobald, 1901

DISTRIBUTION: East Africa, Madagascar, Seychelles; coastal.

CRAB HOSTS: *Sesarma meinerti, S. eulimene.*

TYPE: Semispecific. Predominantly breeds in crabholes; also commonly utilizes ground pools and swamps and rarely natural and artificial containers. The females deposit their eggs on the legs and body of the host. (Goiny et al., 1957; Hogue and Bright, 1971). Females are strongly anthropophilic and vectors of filiariasis in east Africa (Heisch, Goiny and Ikata, 1957).

REFERENCES: Brook Worth et al., 1961 (B); Hopkins, 1952:224; Lumsden, 1955: 170-171 (B).

Subgenus *Stegomyia*

A. aegypti (Linneaus, 1962)

DISTRIBUTION: Cosmopolitan; interior and coastal.

CRAB HOSTS: *Cardisoma armatum, Sesarma africanum.*

TYPE: Transient. Usually breeds in various artificial container habitats. Strongly anthropophilic and vector of yellow fever.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:120; Cheneveau, 1934:590-593; Dalziel, 1920:248, 251-252; Dunn, 1928:249; Riqueau, 1929; Symes, 1960:5, 8; Wanson, 1935:576 (as *argenteus*).

A. africanus (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Accidental. Normally breeds in treeholes. Anthropophilic and vector of yellow fever.

REFERENCE: Wanson, 1935:576-577.

A. luteocephalus (Newstead, 1907)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient or accidental. Normally breeds in treeholes (also in cut bamboo, rockholes and temporary ground pools).

REFERENCES: Dalziel, 1920:251-252; Wanson, 1935:576.

A. polynesiensis Marks, 1951

DISTRIBUTION: South Pacific islands; coastal.

CRAB HOSTS: *Cardisoma carnifex, C. hirtipes.*

TYPE: Semispecific. Usually breeds in containers of various sorts. Strongly anthropophilic and vector of filariasis and dengue. Crabholes important breeding sites when other habitats absent as on low coral islands.

REFERENCES: Belkin, 1962:468, pl. 2; Burnett, 1960; Symes, 1960:5, 8; Tamashiro, 1964:10-11 (B).

A. pseudoscutellaris (Theobald, 1910)

DISTRIBUTION: Fiji; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in containers of various sorts.

REFERENCE: Belkin, 1962:470, pl. 2.

Subgenus *Verralina*

A. butleri Theobald, 1901

DISTRIBUTION: Indomalayan Region; coastal.

CRAB HOST: Not recorded.

TYPE: Probably semispecific. Most commonly known from ground pools in mangroves and nipa palm axils.

REFERENCES: Edwards, 1928:346 (as *umbrosus*); Leicester, 1908:8.

A. parasimilis King and Hoogstraal, 1947

DISTRIBUTION: New Guinea; primarily coastal?

CRAB HOST: Not recorded, "crayfish hole."

TYPE: Transient. Usually breeds in various types of ground pools.

REFERENCES: King and Hoogstraal, 1947:125; van den Assem, 1961:25.

Genus *Anopheles*

Subgenus *Anopheles*

A. tigertti Scanlon and Peyton, 1967

DISTRIBUTION: Thailand; interior.

CRAB HOST: Not recorded. Fresh water species.

TYPE: Semispecific or specific.

REFERENCE: Scanlon and Peyton, 1967.

Subgenus *Cellia*

A. gambiae Giles, 1902, complex.

DISTRIBUTION: Africa; interior and coastal.

CRAB HOSTS: *Cardisoma armatum*, *Sesarma africanum*.

TYPE: Transient. Usually breeds in a wide variety of artificial and natural ground habitats. Anthropophilic and a vector of malaria.

REFERENCES: Aders, 1917:393-394; Bruce-Chwatt and Fitz-John, 1951:120; Cheneveau, 1934:590-593 (as *costalis*); Dalziel, 1920:251-253; Dunn, 1928:249; Ingram and Macfie, 1917:135 (as *costalis*); Macfie and Ingram, 1916:7; Wanson, 1935:576, 578.

Note: The salt water species (?) *merus* (Donitz, 1902) or *melas* (Theobald, 1903) may be found ultimately to be those associated with crabholes (see Coluzzi, 1964).

Subgenus *Nyssorhynchus*

A. albimanus Wiedemann, 1821

DISTRIBUTION: Tropical America, South America; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Accidental. Flushed into crabhole by heavy rains; normally breeds in vegetated ground pools and sluggish streams.

REFERENCES: Shropshire and Zetek, 1927:338 (as *tarsimaculata* in part); Belkin et al., 1970:49.

Genus *Armigeres*

A. breinli (Taylor, 1914)

DISTRIBUTION: New Guinea, Bismark Archipelago, Solomons; primarily coastal.

CRAB HOST: Not recorded.

TYPE: Accidental. Adults only. Species breeds in plant containers and rarely ground pools.

REFERENCES: Peters, 1963:10; Steffan, 1966:215.

Genus *Culex*

Subgenus *Aedinus*

C. bisulcatus (Coquillett, 1906)

DISTRIBUTION: Guadeloupe Island, Lesser Antilles; interior and coastal.
CRAB HOST: Not recorded.
TYPE: Accidental. Normally breeds in bromeliads.
REFERENCE: Floch and Abonnenc, 1945:39.
Note: Probably adults only in crabholes or burrows.

C. corrigani Dyar and Knab, 1907

DISTRIBUTION: Panama; coastal and interior.
CRAB HOST: Not recorded.
TYPE: ? Bionomics poorly known. Type series from bamboo joints.
REFERENCE: Dyar, 1928:347.

C. latisquama (Coquillett, 1906)

DISTRIBUTION: Tropical America; coastal (Atlantic only?)
CRAB HOST: Not recorded.
TYPE: Specific. Multiple collections, all from crabholes.
REFERENCE: Howard, Dyar and Knab, 1915:305.

Subgenus *Culex*

C. annulioris prob. ssp. *consimilis* Newstead, 1907

DISTRIBUTION: Tropical Africa; interior and coastal.
CRAB HOST: *Cardisoma armatum.*
TYPE: Transient. Usually breeds in ground pools.
REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920:253; Wanson, 1935:576, 578.

C. annulirostris Skuse, 1889

DISTRIBUTION: Southern and western Australasian Region, Indonesia, Philippines; interior and coastal.
CRAB HOST: Not recorded.
TYPE: Transient. Indiscriminate breeder; usually breeds in ground pools but also occurs commonly in almost all other habitats.
REFERENCE: Belkin, 1962:pl. 2.

C. carcinoxenus Castro, 1932

DISTRIBUTION: Brazil; coastal.
CRAB HOSTS: *Cardisoma guanhumi, Ucides cordatus.*
TYPE: Specific or semispecific. Known only from crabholes.
REFERENCES: Castro, 1932:97; Forattini, Rabello and Heredia, 1956:85.

C. corniger Theobald, 1903

DISTRIBUTION: American Mediterranean Region.
CRAB HOST: *Ucides cordatus.*
TYPE: Transient. Indiscriminate breeder.
REFERENCES: Howard, Dyar and Knab, 1915:246; Lutz, 1912:19.

C. decens Theobald, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Indiscriminate breeder.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920:251, 253; Dunn, 1928:249.

Note: May be confused with *invidiosus.*

C. duttoni Theobald, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in a wide variety of ground habitats as well as in containers.

REFERENCE: Wanson, 1935:576, 578.

C. foliaceus Lane, 1945

DISTRIBUTION: Brazil; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Probably transient. Bionomics poorly known.

REFERENCE: Stone, 1950:239.

C. habilitator Dyar and Knab, 1906

DISTRIBUTION: Antilles and Trinidad; coastal.

CRAB HOST: Not recorded.

TYPE: Semispecific. Most records from crabholes; also breeds in ground pools and pot holes.

REFERENCES: Bonne and Bonne-Webster, 1925:189; Dyar, 1928:362; Howard, Dyar and Knab, 1915:262 (as *eremita*); Pratt and Seabrook, 1952:27.

C. inflictus Theobald, 1901

DISTRIBUTION: Tropical America; coastal.

CRAB HOST: Not recorded.

TYPE: Specific or semispecific. All records from crabholes.

REFERENCES: Dyar, 1928:391; Hogue and Wirth, 1968:6; Howard, Dyar and Knab, 1915:327 (as *extricator*); Knab, 1910:868-869 (as *extricator*).

Note: A complex of species.

C. invidiosus Theobald, 1901

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Indiscriminate breeder.

REFERENCE: Wanson, 1935:576, 578-579.

Note: May be confused with *decens.*

C. janitor Theobald, 1903

DISTRIBUTION: Greater Antilles; coastal.

CRAB HOST: Not recorded.

TYPE: Specific. Not recorded from other sites.

REFERENCE: Belkin et al., 1970:49; Grabham, 1905:406-407; Hill and Hill, 1948:55.

C. nigripalpus Theobald, 1901

DISTRIBUTION: Tropical America; coastal (Atlantic).

CRAB HOST: Not recorded.

TYPE: Transient. General ground pool breeder, sometimes found in crabholes.

REFERENCES: Belkin et al., 1970:49; Branch and Seabrook, 1959:216; Martini, 1914:70 (as *prasinopleurus*); Pratt et al., 1945:246.

C. perfuscus Edwards, 1914

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in ground pools.

REFERENCE: Wanson, 1935:576, 578-579.

C. philipi Edwards, 1929

DISTRIBUTION: Western tropical Africa; interior? and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Type series bred from larvae found in crabholes. Also found in vegetated pools.

REFERENCE: Edwards, 1929:327.

C. pipiens quinquefasciatus Say, 1823

DISTRIBUTION: Cosmopolitan; interior and coastal.

CRAB HOSTS: *Cardisoma armatum, Sudanonautes africanus.*

TYPE: Transient. Usually breeds in foul ground pools and ditches and large artificial containers. Vector of filariasis over wide areas of world.

REFERENCES: Dunn, 1928:249; Hanney, 1960:99; Wanson, 1935:576, 578-579.

C. pruina Theobald, 1901

DISTRIBUTION: Western and central Africa; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in ground pools with decaying leaves.

REFERENCE: Dunn, 1928:249.

C. scimitar Branch and Seabrook, 1959

DISTRIBUTION: Bahamas, small islands.

CRAB HOST: Not recorded.

TYPE: Transient? Bionomics poorly known; recorded also from ground pools.

REFERENCE: Branch and Seabrook, 1959:216.

C. sitiens Wiedmann, 1828

DISTRIBUTION: Oriental Region, east Africa and western Pacific; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Normally breeds in saline or brackish coastal ground waters. Anthropophilic.

REFERENCE: van Someren et al., 1955:487.

C. thalassius Theobald, 1903

DISTRIBUTION: Tropical Ethiopian Region; coastal.

CRAB HOST: *Cardisoma armatum, Uca tangeri, Sesarma africanum.*

TYPE: Semispecific. Multiple records from crabholes. Also breeds commonly in saline ground pools and artificial containers. Strongly anthropophilic.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119-120; Dalziel, 1920:251-253; Hopkins, 1952:286; Ingram and Macfie, 1917:147-149; Wanson, 1935:576, 578-579.

Subgenus *Culiciomyia*

C. cinerellus Edwards, 1922

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Semispecific or transient. Numerous records from crabholes.

REFERENCES: Dalziel, 1920:251-253 (as *nebulosus*); Dunn, 1928:249; Edwards, 1929:327; Wanson, 1935:578.

C. nailoni King and Hoogstraal, 1946

DISTRIBUTION: New Guinea; interior and coastal.

CRAB HOST: Not recorded, "crabhole in rain forest."

TYPE: ? Bionomics insufficiently known. One record from crabhole.

REFERENCE: King and Hoogstraal, 1946b.

C. ruthi Peters, 1958

DISTRIBUTION: New Guinea; coastal.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. Adults only, captured at the entrance of small crabholes in partial shade on the beach. Immatures unknown.

REFERENCE: Steffan, 1966:219.

C. spathifurca (Edwards, 1915)

DISTRIBUTION: Oriental and Indomalayan Regions; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. A general ground pool breeder.

REFERENCE: Carter and Wijesundara, 1948:145 (as *stylifurcatus*).

Subgenus *Lophoceraomyia*

C. becki Belkin, 1962

DISTRIBUTION: Solomons; small islands.
CRAB HOST: Not recorded.
TYPE: Specific. Known only from crabholes.
REFERENCE: Belkin, 1962:266, pl. 2.

C. infantulus Edwards, 1922

DISTRIBUTION: Oriental (including Japan) and Indomalayan Regions; primarily coastal (?)
CRAB HOST: Not recorded.
TYPE: Transient. A general ground pool and container breeder.
REFERENCE: Bram, 1967:61.

C. pholeter Bram and Rattanarithikul, 1967

DISTRIBUTION: Thailand; interior.
CRAB HOST: Not recorded.
TYPE: Specific. Collected repeatedly and exclusively from small crabholes in secondary rain forests in mountainous terrain.
REFERENCE: Bram and Rattanarithikul, 1967:13.

C. reidi, Colless, 1965

DISTRIBUTION: Singapore, Selangor; coastal.
CRAB HOST: Not recorded.
TYPE: Transient. Usually breeds in shaded pools at margin of tidal zone.
REFERENCE: Colless, 1965:280.

C. rubithoracis (Leicester, 1908)

DISTRIBUTION: Indomalayan Region, Japan; interior and coastal.
CRAB HOST: Not recorded.
TYPE: Transient. Ground pool breeder.
REFERENCE: Macdonald, 1957:29.

C. variatus (Leicester, 1908)

DISTRIBUTION: Indomalayan Region; coastal.
CRAB HOST: Not recorded.
TYPE: Transient. Usually breeds in ground pools but also utilizes containers near the ground.
REFERENCE: Colless, 1965:273.

Subgenus *Lutzia*

C. tigripes Grandpre and Charmoy, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.
CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Indiscriminate breeder. Larva predaceous.
REFERENCE: Wanson, 1935:578.

Subgenus *Melanoconion*

C. opisthopus Komp, 1926

DISTRIBUTION: Tropical America; coastal (Atlantic).
CRAB HOST: *Cardisoma guanhumi.*
TYPE: Accidental. Probably normal breeding site deep seepage channels or solution holes in coral.
REFERENCES: Pratt et al., 1945:246; Stone and Hair, 1968:41 (as *cedecei*); Belkin, 1969 (T).

C. carcinophilus Dyar and Knab, 1906

DISTRIBUTION: Dominican Republic, ? Guatemala, Cuba; coastal.
CRAB HOST: *Cardisoma guanhumi.*
TYPE: Specific.
REFERENCES: Dyar and Knab, 1906:220; Montchadsky and Garcia, 1966:46.

C. iolambdis Dyar, 1918

DISTRIBUTION: Tropical America; primarily coastal (Atlantic).
CRAB HOST: Not recorded.
TYPE: Transient. Usually breeds in coastal ground pools shaded by mangroves.
REFERENCE: Pratt and Seabrook, 1952:27.

C. nicaroensis Duret, 1967

DISTRIBUTION: Cuba; coastal.
CRAB HOST: Not recorded.
TYPE: ?
REFERENCE: Duret, 1967:80.

Subgenus *Mochthogenes*

C. inconspicuosus (Theobald, 1908)

DISTRIBUTION: Ethiopian Region; interior and coastal.
CRAB HOST: *Cardisoma armatum.*
TYPE: Transient. Usually breeds in nearly stagnant pools, in streams and in ground pools.
REFERENCE: Dalziel, 1920:251-252, 254.

C. laureli Baisas, 1935

DISTRIBUTION: Philippines; interior and coastal.
CRAB HOST: Not recorded.
TYPE: Transient. Usually breeds in small vegetated ground pools.
REFERENCE: Delfinado, 1966:133.

Subgenus *Neoculex*

C. insignis (Carter, 1911)

DISTRIBUTION: Africa; interior and coastal.

CRAB HOST: *Sudanonautes africanus, Cardisoma armatum.*

TYPE: Transient. Usually breeds in foul water in pooled streams.

REFERENCES: Dalziel, 1920:251-253; Dunn, 1928:249; Hanney, 1960: 99; Macfie and Ingram, 1916:11.

C. rima Theobald, 1901

DISTRIBUTION: West and central Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Specific or semispecific. Multiple records only from crabholes.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920: 251-253; Philip, 1931:192; Surtees, 1958:90; Wanson, 1935:576, 578.

C. salisburiensis Theobald, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in forest ground pools and streams.

REFERENCE: Dalziel, 1920:251-253.

Genus *Deinocerites*

GENERAL REFERENCES: Adames, 1971; Belkin and Hogue, 1959.

Deinocerites normally breeds in crabholes. Referred to as "Crabhole Mosquitoes" in the literature they unquestionably are specific members of the crabhole community, being found breeding outside this habitat only very rarely in such related or proximate places as mangrove treeholes, mangrove pot holes and coastal ground pools.

The genus ranges throughout the American tropics, each species having a completely Atlantic or Pacific (with a few exceptions) distribution. Curiously, in spite of the occurrence of suitable habitats and hosts (*Cardisoma* and *Ucides*) along the entire Brazilian coast to São Paulo, the most southernly Atlantic record is on the coast of the State of Maranhão (Cerqueira, 1938: 291). This apparent truncation in the distribution may be due only to lack of collecting.

All stages exhibit unique characteristics among the Culicidae; some are definitely functional in their relationship to the crabhole habitat and community. The peculiar pupal attendance and mating behavior first described in detail in *Deinocerites cancer* (Downes, 1966; Provost and Haeger, 1967) represents an adaptation correlated with a non-dispersing evolutionary trend in this line of mosquitoes. Among the immatures the larvae of all species have lateral head pouches of unknown function and the pupae of some have three float hairs (these and others discussed by Belkin and Hogue, 1959:421).

Only occasional specimens are observed biting man. The normal food is probably reptile, amphibian or bird blood (Templis and Galindo, 1970).

Deinocerites cancer, at least in Florida (Haeger and Phinizee, 1959), is known to be autogenous.

D. atlanticus Adames, 1971

CRAB HOST: Not recorded. Known from small crabholes.

D. barretoi Adames, 1971

CRAB HOST: Not recorded.

D. belkini Adames, 1971

CRAB HOST: Not recorded, *Uca* (?)

D. cancer Theobald, 1901

CRAB HOST: *Cardisoma guanhumi.*

REFERENCES: Downes, 1966 (B); Haeger and Phinizee, 1959 (B); Komp, 1956; Provost and Haeger, 1967 (B).

D. colombianus Adames, 1971

CRAB HOST: Not recorded.

D. costaricensis Adames and Hogue, 1970

CRAB HOST: *Cardisoma crassum.*

D. curiche Adames, 1971

CRAB HOST: Not recorded.

D. dyari Belkin and Hogue, 1959

CRAB HOST: Not recorded.

D. epitedeus (Knab, 1907)

CRAB HOST: Not recorded.

D. howardi Belkin and Hogue, 1959

CRAB HOST: Not recorded.

D. mathesoni Belkin and Hogue, 1959

CRAB HOSTS: *Uca pugilator, U. subcylindrica, Gecarcinus lateralis.*

REFERENCES: Fisk, 1941 (as *spanius*) (B); Peyton et al., 1964 (B).

D. magnus (Theobald, 1901)

CRAB HOST: Not recorded.

D. melanophyllum Dyar and Knab, 1907

CRAB HOST: Not recorded.

D. mcdonaldi Belkin and Hogue, 1959

CRAB HOST: Not recorded.

D. nicoyae Adames and Hogue, 1970

CRAB HOST: *Ucides occidentalis.*

D. panamensis Adames, 1971

CRAB HOST: Not recorded.

D. pseudes Dyar and Knab, 1909

CRAB HOSTS: *Cardisoma crassum, C. guanhumi, Uca subcylindrica, Gecarcinus lateralis.*

REFERENCES: Galindo, 1967 (B); Hogue and Wirth, 1968; Peyton et al., 1964 (B).

D. spanius (Dyar and Knab, 1909)

CRAB HOST: Not recorded.

Genus *Eretmapodites*

E. quinquevittatus Theobald, 1901

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Accidental. Adults only. Apparently normally breeds in empty *Achatina* shells (land snails).

REFERENCE: Wanson, 1935:576.

Genus *Galindomyia*

G. leei Stone and Barreto, 1969

DISTRIBUTION: Colombia; coastal.

CRAB HOST: Not recorded.

TYPE: Probably specific, though adults only known from crabholes.

REFERENCE: Stone and Barreto, 1969.

Genus *Hodgesia*

H. nigeriae Edwards, 1930

DISTRIBUTION: West tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Accidental. Biology not known; probably breeds in vegetated jungle pools like its relatives.

REFERENCE: Wanson, 1935:576-577, 579.

Genera *Mansonia* and *Coquillettidia*

All occurrences of *Mansonia* and *Coquillettidia* are resting adults only and constitute accidental utilization of the crabhole habitat. The larvae of all members of these genera are associated strictly with floating and emergent water plants from which they obtain oxygen with a specially modified, piercing siphon.

C. aurites (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

REFERENCE: Wanson, 1935:576.

Note: Anthropophilic.

M. africana (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

REFERENCE: Dalziel, 1920:253.

Note: Anthropophilic and vector of yellow fever and filariasis.

M. uniformis (Theobald, 1901)

DISTRIBUTION: Widespread throughout Old World Tropics; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

REFERENCE: Wanson, 1935:576.

Note: Anthropophilic and important vector of filariasis.

Genus *Psorophora*

P. confinnis (Lynch Arribalzaga, 1891)

DISTRIBUTION: Eastern and southern United States, Caribbean, eastern South America to Argentina; interior and coastal.

CRAB HOST: *Cambarus diogenes ludovicianus.*

TYPE: Transient. Usually breeds in shallow ground pools.

REFERENCE: Evan, 1962.

Note: A complex of species.

Genus *Uranotaenia*

Nearly all the records in this genus are from the burrows of freshwater crabs. See Peyton, 1970.

U. alboabdominalis Theobald, 1910

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Sudanonautes africanus.*

TYPE: Transient. Adults only. A ground pool breeder.

REFERENCE: Hanney, 1960:99.

U. annulata Theobald, 1901

DISTRIBUTION: Western tropical Africa; interior and coastal.

CRAB HOSTS: *Cardisoma armatum, Sudanonautes africanus.*

TYPE: Specific or semispecific. Many records and collections, all from crabholes.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920: 251, 253 (as *fasciata*); Dunn, 1928:249; Hanney, 1960:99; Hopkins, 1952:59; Macfie and Ingram, 1916:7; Philip, 1931:192; Surtees, 1958:91.

U. atra Theobald, 1905

DISTRIBUTION: New Guinea, Bismark Archipelago; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in plant and artificial containers and ground pools and in sago palm swamps.

REFERENCES: van den Assem, 1961:25; Steffan, 1966:203.

U. bilineata var. *fraseri* Edwards, 1912

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Accidental? Probably normally breeds in grass-grown ground pools.

REFERENCE: Dalziel, 1920:251-253.

U. bicolor Leicester, 1908

DISTRIBUTION: Southeast Asia; interior.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in a wide variety of ground pools.

REFERENCE: Peyton, 1970:3 and personal communication.

U. caliginosa Philip, 1931

DISTRIBUTION: Nigeria; interior.

CRAB HOST: Not recorded.

TYPE: ?

REFERENCE: Philip, 1931:190.

U. husaini Qutubuddin, 1946 (1947)

DISTRIBUTION: India; interior.

CRAB HOST: Not recorded.

TYPE: ? Adults only. Bionomics insufficiently known.

REFERENCE: Qutubuddin, 1946 (1947):118.

U. koli Peyton, 1970

DISTRIBUTION: Cambodia, Thailand; interior.

CRAB HOST: Not recorded. Fresh water species.

TYPE: Specific or semispecific.

REFERENCE: Peyton and Klein, 1970:248.

U. lateralis Leicester, 1908

DISTRIBUTION: Indomalayan, north Australian and Papuan Regions; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in slightly brackish open pools behind beaches, although may be very common in crabholes.

REFERENCE: Leicester, 1908:8, 217 (as *cancer*).

U. mashonaensis Theobald, 1901

DISTRIBUTION: Tropical Africa, Madagascar; interior and coastal.

CRAB HOST: *Sudanonautes africanus.*

TYPE: Accidental. Adults only. Breeds in various ground habitats (swamps, rockpools, pools, etc.).

REFERENCE: Hanney, 1960:99.

U. mattinglyi Qutubuddin, 1951

DISTRIBUTION: India; interior.

CRAB HOST: Not recorded.

TYPE: ? Adults only. Bionomics insufficiently known. "Habitat: caught from crabholes in an old pond in the Public Garden, Hyderabad (Deccan) City, India, in October, 1943."

REFERENCE: Qutubuddin, 1951:107.

U. montana Ingram and de Meillon, 1927

DISTRIBUTION: Natal, Transvaal, Cape Province; coastal?

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. A single record from crabholes. The larva recorded by Hopkins was collected from a crabhole and lived in captivity for 4½ months before pupating.

REFERENCE: Hopkins, 1952:58.

U. nivipous Theobald, 1912

DISTRIBUTION: Tropical Africa; coastal? or interior by large rivers?

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. Two records only from crabholes.

REFERENCES: Ingram and de Meillon, 1927 (as *candidipes*); Surtees, 1958:91 (as *candidipes*).

U. philippinensis Delfinado, 1966

DISTRIBUTION: Philippines; interior.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known.

REFERENCE: Peyton, 1970:3 and personal communication.

U. rossi Delfinado, 1966

DISTRIBUTION: Philippines; interior.

CRAB HOST: Not recorded.

TYPE: Specific or semispecific. Numerous collections all from crabholes.

REFERENCE: Peyton, 1970:3 and personal communication.

Family CHAOBORIDAE

The larvae of phantom midges are all aquatic, usually being encountered in fresh water ponds and lakes. Those of two species in the genus *Corethrella* are recorded from crabholes.

Genus *Corethrella*

C. stonei Lane, 1942

DISTRIBUTION: Panama; coastal.

CRAB HOST: *Cardisoma* sp. (*guanhumi?*)

TYPE: ? Bionomics insufficiently known. Adults only, taken at mouths of crabholes.

REFERENCE: Lane, 1942:119.

C. tripunctata Lane, 1942

DISTRIBUTION: Trinidad, Puerto Rico, Brazil; coastal?

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. Larvae found in crabholes beneath rocks, 100 feet elevation.

REFERENCE: Lane, 1942:120.

Family CERATOPOGONIDAE

A few species of this family, all in the genus *Culicoides*, are recorded as breeding in crabholes. Certainly many more of these coastal, salt marsh and tidal flat-loving flies will be found utilizing the crabhole habitat.

Genus *Culicoides*

C. arubae Fox and Hoffman, 1944

DISTRIBUTION: American Tropics; coastal.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known.

REFERENCE: Fox and Hoffman, 1944:109.

C. cancer Hogue and Wirth, 1968

DISTRIBUTION: Costa Rica; coastal (Pacific).

CRAB HOSTS: *Cardisoma crassum, Ucides occidentalis.*

TYPE: Specific. The species has been collected in all stages numerous times and in very large numbers only from crabholes.

REFERENCE: Hogue and Wirth, 1968 (G).

C. cancrisocius Macfie, 1946

DISTRIBUTION: Fiji Islands; coastal.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known.

REFERENCES: Macfie, 1946; Wirth and Arnaud, 1969:517-518.

C. distinctipennis Austen, 1912

DISTRIBUTION: Nigeria, Uganda, Gold Coast, Senegal; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE:? Bionomics insufficiently known.

REFERENCE: Wanson, 1935:579, 584 (as *wansoni*).

C. insignis Lutz, 1913

DISTRIBUTION: Mesoamerica; coastal.

CRAB HOST: *Ucides cordatus.*

TYPE: Transient. Usually breeds in coastal marshes.

REFERENCES: Forattini et al., 1956:197 (B,D); Forattini et al., 1958: 37 (B, D).

C. reticulatus Lutz, 1913

DISTRIBUTION: Brazil, Panama; coastal.
CRAB HOST: *Cardisoma guanhumi.*
TYPE: Specific or semispecific. Numerous collections, all from crabholes.
REFERENCES: Forattini et al., 1957:312 (B,D); Lutz, 1912:19, 1913: 50 (B).

Family DROSOPHILIDAE

Two species of *Drosophila* have developed a symbiotic association with land crabs of the genus *Gecarcinus.* The larvae live on the crabs and even pupate (in one species) on the third maxilliped. The adult flies have been observed to remain on the crab, running over and hovering about the carapace. Though the food of the larvae is not known with certainty, it probably consists of food leavings of the host in one case and the host's tissues in the other.

Genus *Drosophila*

D. carcinophila Wheeler, 1960

DISTRIBUTION: Greater and Lesser Antilles, Bahamas, Providencia; islands only (coastal on large islands).
CRAB HOST: *Gecarcinus ruricola.*
TYPE: Commensal, larva in renal grooves and peribuccal region.
REFERENCES: Carson, 1967 (B,D); Wheeler, 1960 (B,D).

D. endobranchia Carson and Wheeler, 1968

DISTRIBUTION: Cayman Islands; small islands.
CRAB HOSTS: *Gecarcinus ruricola* and *lateralis.*
TYPE: Parasitic, larva on host's gills.
REFERENCE: Carson and Wheeler, 1968 (B,D).

MISCELLANEOUS DIPTERA

A number of shore inhabiting flies have been taken, usually as adults only, from the mouths of crabholes. Others (species largely unidentified) are known in the immature stages from water in the burrow.

Family CHIRONOMIDAE

Species undetermined.

LOCALITIES: Lagos, Nigeria; Banana, Congo.
CRAB HOST: *Cardisoma armatum.*
TYPE: ?
REFERENCES: Bruce-Chwatt and Fitz-John, 1951:118; Wanson, 1935: 578.

Family CHLOROPIDAE

Genus *Lasiopleura* sp.

LOCALITY: Not specified.
CRAB HOST: Not recorded.
TYPE: ?
REFERENCE: Wheeler, 1960:210.

Family DOLICHOPODIDAE

Asydetus carcinophilus Parent, 1937

DISTRIBUTION: Hawaii; coastal.
CRAB HOST: *Ocypode ceratophthalma.*
TYPE: Transient. Adults rest and hide in the burrow mouth. Immatures undoubtedly develop elsewhere.
REFERENCES: Wheeler, 1960:210; Williams, 1938:126-129.

Family EMPIDIDAE

Chersodromia hawaiiensis Melander, 1938

DISTRIBUTION: Hawaii; coastal.
CRAB HOST: Not recorded, probably *Ocypode.*
TYPE: Transient. Adults found on the beach in the near vicinity of burrows.
REFERENCE: Melander, 1938:57.

Family EPHYDRIDAE

Hecamede sp.

LOCALITY: Not specified.
CRAB HOST: Not recorded.
TYPE: ?
REFERENCE: Wheeler, 1960:210.

Undetermined "larva A"

LOCALITY: Admiralty Islands.
CRAB HOST: *Cardisoma hirtipes.*
TYPE: Symbiosis? Larvae found in branchial chambers of preserved crabs.
REFERENCES: Baylis, 1915; Keilin, 1921.

Undetermined "larva B"

LOCALITY: Christmas Island (Indian Ocean).
CRAB HOST: *Gecarcoidea lalandii (humei).*
TYPE: Symbiosis? Larvae found in branchial chambers of preserved crabs.
REFERENCES: Baylis, 1915; Keilin, 1921.

Family TETHINIDAE

Rhicnoessa sp.

LOCALITY: Not specified.
CRAB HOST: Not recorded.
TYPE: ?
REFERENCE: Wheeler, 1960:210.

Order COLEOPTERA

Family DYTISCIDAE

Bidessus rogersi Young, 1941

DISTRIBUTION: Florida; interior.
CRAB HOST: *Procambarus rogersi rogersi.*
TYPE: Transient. Primarily a flatwoods species occurring in slow streams, ditches, cypress swamps, ponds, and other lenitic situations.
REFERENCE: Young, 1954:17, 64-65.

Family HELODIDAE

Helodes ? sp.

LOCALITY: Costa Rica.
CRAB HOST: *Cardisoma crassum.*
TYPE: ? Bionomics insufficiently known. Larva only.
REFERENCE: Hogue and Wirth, 1968:6.

MISCELLANEOUS INSECTS

Order HEMIPTERA

Family GELASTOCORIDAE

Mononyx grandicollis Germar, 1840

DISTRIBUTION: West Africa; interior and coastal?
CRAB HOST: *Sudanonautes africanus.*
TYPE: Transient or accidental. A streamside mud flat inhabitant.
REFERENCE: Hanney, 1960:100.

Family VELIIDAE

Microvelia oraria Drake, 1952

DISTRIBUTION: Costa Rica.
CRAB HOST: Not recorded.
TYPE: ?
REFERENCE: Drake, 1952:14-15.

Family CYDNIDAE

Sehirus tibialis Stal, 1853

DISTRIBUTION: West Africa; interior and coastal?
CRAB HOST: *Sudanonautes africanus.*
TYPE: Accidental. Ground burrowing species.
REFERENCE: Hanney, 1960:100 (as *Legnotus tibialis*).

Order ACARINA

Two mites of different families are known as symbiotic associates of certain land crabs:

Family TYROGLYPHIDAE

Rhizoglyphus sp.

DISTRIBUTION: Dry Tortugas Islands; small islands.
CRAB HOST: *Gecarcinus lateralis.*
TYPE: Commensal or parasitic. Single nymphal specimen known.
REFERENCE: Pearse, 1929:230.

Family LAELAPTIDAE

Laelaps cancer Pearse, 1929

DISTRIBUTION: Dry Tortugas Islands; small islands.
CRAB HOST: *Gecarcinus lateralis.*
TYPE: Commensal or parasitic. All stages found in branchial chambers and on gills.
REFERENCES: Pearse, 1929:229-230; 1932:112.

Family UNDETERMINED

Species Undetermined

LOCALITY: West Indies.
CRAB HOST: *Gecarcinus ruricola.*
TYPE: ?
REFERENCE: Carson, 1967:342.

Class CRUSTACEA

Apart from the crab host itself, certain other aquatic crustacea appear to be members of the crabhole community.

Order COPEPODA

Cancrincola jamaicensis Wilson, 1913

DISTRIBUTION: Jamaica, Key West; coastal.
CRAB HOST: *Cardisoma guanhumi.*
TYPE: Parasitic? Cling to gill filaments of crab with their second antennae and maxillipeds. Probably feed on host's blood or secretions.
REFERENCES: Pearse, 1932:112; Wilson, 1913:264-268.

Order EUCOPEPODA

Cyclops sp.

LOCALITIES: Lagos, Nigeria; Banana, Congo.
CRAB HOST: *Cardisoma armatum.*
TYPE: ?
REFERENCES: Bruce-Chwatt and Fitz-John, 1951:118; Wanson, 1935: 578.

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